

Longitudinal Study of Dental Development in Chimpanzees of Known Chronological Age: Implications for Understanding the Age at Death of Plio-Pleistocene Hominids

ROBERT L. ANEMONE, MARK P. MOONEY, AND MICHAEL I. SIEGEL
Department of Anthropology, State University of New York, Geneseo, New York 14454 (R.L.A.); Departments of Anatomy and Histology (M.P.M.), Orthodontics (M.I.S.), and Anthropology (M.P.M., M.I.S.), University of Pittsburgh, Pittsburgh, PA 15260

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ABSTRACT Reconstruction of life history variables of fossil hominids on the basis of dental development requires understanding of and comparison with the pattern and timing of dental development among both living humans and pongids. Whether dental development among living apes or humans provides a better model for comparison with that of Plio-Pleistocene hominids of the genus *Australopithecus* remains a contentious point. This paper presents new data on chimpanzees documenting developmental differences in the dentitions of modern humans and apes and discusses their significance in light of recent controversies over the human or pongid nature of australopithecine dental development. Longitudinal analysis of 299 lateral head radiographs from 33 lab-reared chimpanzees (*Pan troglodytes*) of known chronological age allows estimation of means and standard deviations for the age at first appearance of 8 developmental stages in the mandibular molar dentition. Results are compared with published studies of dental development among apes and with published standards for humans. Chimpanzees are distinctly different from humans in two important aspects of dental development. Relative to humans, chimpanzees show advanced molar development vis a vis anterior tooth development, and chimpanzees are characterized by temporal overlap in the calcification of adjacent molar crowns, while humans show moderate to long temporal gaps between the calcification of adjacent molar crowns. In combination with recent work on enamel incremental markers and CAT scans of developing dentitions of Plio-Pleistocene hominids, this evidence supports an interpretation of a rapid, essentially “apelike” ontogeny among australopithecines. © 1996 Wiley-Liss, Inc.

Ever since the work of Adolf Schultz (e.g., Schultz, 1969), primatologists have been aware that one of the distinctive traits of the primates is a trend towards prolongation of ontogeny. As one ascends the “Scala Naturae” of the primate order from prosimians to monkeys and apes and finally to humans, an increased absolute amount of time is devoted to each of the primary periods of ontog-

eny: gestation, infancy, childhood, and adulthood (Fig. 1). Ecological theory suggests that this pattern reflects an increasingly K-selected strategy on the part of the primates,

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Address reprint requests to Dr. Robert L. Anemone, Department of Anthropology, SUNY at Geneseo, Geneseo, NY 14454.

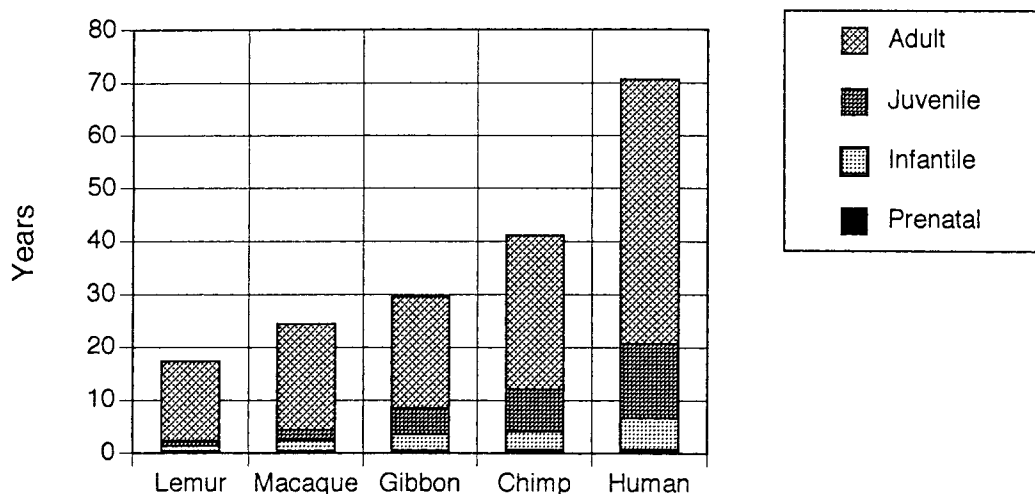


Fig. 1. Progressive prolongation of the primary periods of ontogeny is a characteristic of the primate order. Bogin (1988:60) suggests that human ontogeny uniquely includes the addition of childhood "as a period of growth between infancy and juvenescence (the start of the juvenile growth period), thus remaining dependent upon adult caregiving for a relatively and absolutely longer time than any other primate." (After Schultz, 1969).

including other features such as parental care, small litter size, large body size, and big brains (Barash, 1982). Anthropological, and especially paleoanthropological, theory suggests that the extremely prolonged ontogenetic development that characterizes *Homo sapiens* warrants a separate and unique explanation.

The functional and evolutionary significance of a prolonged period of childhood dependency among humans, has long been a favorite topic of speculation among anthropologists (e.g., Lovejoy, 1981; Bogin, 1988) and others interested in human evolution (e.g., Gould, 1977). Most authorities would agree that the long human childhood is associated with the complexities involved in the individual's acquisition of culture and especially of language (Bogin, 1988; Tanner, 1990). Dobzhansky (1962:58) argued many years ago that "although a prolonged period of juvenile helplessness and dependency would, by itself, be disadvantageous to a species because it endangers the young and handicaps their parents, it is a help to man because the slow development provides time for learning and training, which are far more extensive and important in man than in any other animal." The clear implication of this

statement is that by understanding the ontogenetic development of our fossil ancestors, we may be able to recognize the critical biobehavioral shifts that resulted in the origin of the culture bearing, language using, tool manufacturing way of life that makes humans unique.

In the 1970s, Alan Mann of the University of Pennsylvania laid the foundation for all subsequent studies of dental development and life history reconstruction among fossil hominids. Working on the juvenile dentitions of robust australopithecines from the South African cave site of Swartkrans, Mann (1975) noted similarities between the fossils and modern humans in the development and emergence of the permanent molar dentition and in characteristic patterns of tooth wear. He concluded that australopithecines shared the distinctive human rate of slow or prolonged dental development, suggesting that they resembled humans in having a prolonged period of childhood dependency. Mann's estimates of age at death among australopithecines were thus based on schedules of dental development in modern humans, and reflected his belief that the major stages of life had a similar duration among both modern and Plio-Pleistocene hominids.

Reasoning that a long period of childhood dependency is best explained as an adaptation for learning the skills involved in tool manufacture, Mann (1975:84) stated that the evidence of prolonged dental development among australopithecines is "the first direct morphological data for the presence of culture in this hominid group." In spite of the lack of secure archaeological evidence of australopithecine stone tool manufacture, Mann's conclusions have been widely reported and extremely influential in the field of Paleoanthropology (see Susman, 1994, for a recent "morphological" argument for stone tool manufacture among robust australopithecines, based on the anatomy of the thumb and hand in Swartkrans hominids).

Recently a number of workers have questioned this interpretation of australopithecine dental development and life history based on a wealth of new data resulting from the application of innovative histological, microscopic, and comparative approaches to the problem of determining absolute timing of dental development (for reviews, see Dean, 1987b; Beynon and Dean, 1988; Smith, 1992). Examination of incremental growth markers in dental enamel (e.g., cross-striations and Striae of Retzius) has led to new estimates of tooth formation time and age at death among fossil hominids (Beynon and Dean, 1987, 1988; Beynon and Wood, 1987; Bromage, 1987; Bromage and Dean, 1985; Dean, 1987a, 1989; Dean et al., 1993; Ramirez-Rozzi, 1993a,b). The data indicate that australopithecine (*sensu lato*) dental development may have occurred during a shorter (i.e., more apelike) period of time than occurs in modern humans, and that emergence of the first permanent molars occurred among these fossil hominids between 3 and 4 years of age as in modern apes (Nissen and Riesen, 1964), rather than 5 and 6 years as in humans (Demirjian, 1986). This interpretation is supported by comparative analyses of the pattern of dental development in humans, apes, and fossil hominids (Smith, 1986, 1987, 1988, 1991a). The important implication of this new view is that the critical ontogenetic shift in hominids and its bio-behavioral sequelae like tool use, language, and culture must have occurred after the australopithecine stage

of human evolution. Smith's (*op. cit.*) work suggests that even *Homo habilis* may have retained patterns of dental development strikingly similar to modern pongids. If early hominid life history closely resembled that of modern apes, reconstructions of their behavior and ecology based on modern human analogies are likely to be inaccurate.

In addition to some persistent doubts concerning the temporal periodicity of enamel incremental markers (critically reviewed in Mann et al., 1990), controversy remains in describing the nature of developmental differences between the dentitions of living apes and humans and in determining which of these groups provides a better model for comparison of pattern and timing of dental development among Plio-Pleistocene hominids (Lewin, 1987; Mann, 1988; Mann et al., 1987; Smith, 1987, 1991b; Simpson et al., 1990; Anemone and Watts, 1992). The distinction between pattern and timing is critical, since there is no *a priori* basis for inferring timing from pattern or sequence of events in the growth and development of dentitions. Most primates are broadly similar in pattern of development in most anatomical systems, for example, skeletal, dental, and reproductive systems (Schultz, 1969; Smith, 1992). The differences within the order appear in relative and absolute duration of growth, as well as in growth velocity. Thus, one cannot conclude that the rate of australopithecine dental development resembled that of humans or of apes solely on the basis of pattern similarities (*contra* Mann, 1975). One approach to this problem involves comparison of both pattern and timing of dental development through analysis of dental radiographs. While good standards of dental development exist for European and North American populations of *Homo sapiens* (Demirjian, 1986; Fanning, 1961; Fanning and Moorrees, 1969; Moorrees et al., 1963; Nolla, 1960; Schour and Massler, 1940a,b), few data have been published on the subject of the development of the ape dentition (Nissen and Riesen, 1945, 1964; Dean and Wood, 1981; Anemone et al., 1991; Conroy and Mahoney, 1991; Kuykendall et al., 1992).

The most commonly cited reference on pongid dental development, and the first

reasonably successful attempt at developing standards of dental development among apes for comparison with the well known human standards, was the pioneering contribution of Dean and Wood (1981). These authors made a radiographic analysis of a cross sectional sample of the skulls and jaws of 175 juvenile apes (chimpanzees, gorillas, and orangutans). Since the subjects of Dean and Wood's study were wild shot museum specimens, their chronological ages were unknown. Dean and Wood's analytical approach purposely minimized within group variation and sought to portray a modal or archetypal pattern of dental development by excluding radiographs with teeth whose status was intermediate between the 9 named developmental stages they used. Extrapolating from published data on age at emergence into the oral cavity of the chimpanzee deciduous and permanent dentitions (Nissen and Riesen, 1945, 1964), Dean and Wood (1981) created a chart of ape dental development that has played an important role in the comparison of fossil hominid dentitions with those of modern pongids (Smith, 1986, 1991a). Perhaps their most significant result (since confirmed by elegant histological work reported in Beynon et al., 1991; Dean and Beynon, 1991) was the suggestion that the major difference in the duration of human and ape dental development was determined to a great extent by differences in rates of root growth, which are fast in apes and slow in humans.

Several recent studies have examined dental development (Anemone et al., 1991) and tooth emergence (Conroy and Mahoney, 1991; Kuykendall et al., 1992) on mixed-longitudinal samples of lab-reared chimpanzees of known chronological ages. Anemone et al. (1991) revised Dean and Wood's (1981) chart of pongid dental development based on examination of 99 lateral head radiographs of 16 chimpanzees from the Yerkes Laboratories of Primate Biology in Orange Park, Florida (now the Yerkes Regional Primate Center in Atlanta, Georgia), and suggested two major distinctions in pattern and timing of dental development of humans and chimpanzees. First, human molar development is greatly delayed compared to that of chimpanzees. This pattern is clear at the time of

emergence of the M1 into the oral cavity, at 3–4 years of age in chimpanzees and 5–6 years of age in humans. At this time, human incisors and canines have complete crowns and significant root development, while chimpanzee incisors and canines are less than crown complete. Second, while temporal gaps exist between periods of calcification of adjacent molar crowns in humans, chimpanzees are characterized by marked temporal overlap in calcification of adjacent molar crowns. Thus, in chimpanzees, long before the first molar is crown complete, the second molar already shows initial crown calcification. The same pattern characterizes the developmental relationships of the second and third molars. Obvious limitations of the Yerkes study included a small sample size of chimpanzees ($N = 16$) and of radiographs ($N = 99$), which made it impossible to calculate variation in the timing of chimpanzee dental development. Conroy and Mahoney (1991) and Kuykendall et al. (1992) examined patterns of tooth emergence in 58 chimpanzees of known chronological age from the Laboratory for Experimental Medicine and Surgery in Primates (LEMSIP) in Tuxedo, New York. Their results also support differences in relative rates of development (as measured by emergence into the oral cavity) of anterior and posterior teeth between humans and chimpanzees. Humans are characterized by emergence of the first incisor prior to the first molar, and of the canine prior to the second molar, while chimpanzees consistently reverse these developmental relationships.

The present study attempts to increase our knowledge base of pongid dental development through analysis of another mixed longitudinal sample of chimpanzees of known chronological age. This study provides, for the first time, estimation of both central tendency and dispersion for calcification of ape dentition, and thus allows for more realistic and useful comparisons with human dental development. Ultimately, resolution of current controversies concerning the ape or human nature of dental development (and, consequently, of life history in general) among fossil hominids will be resolved by analysis of the fossil data in reference to clear standards of growth and devel-

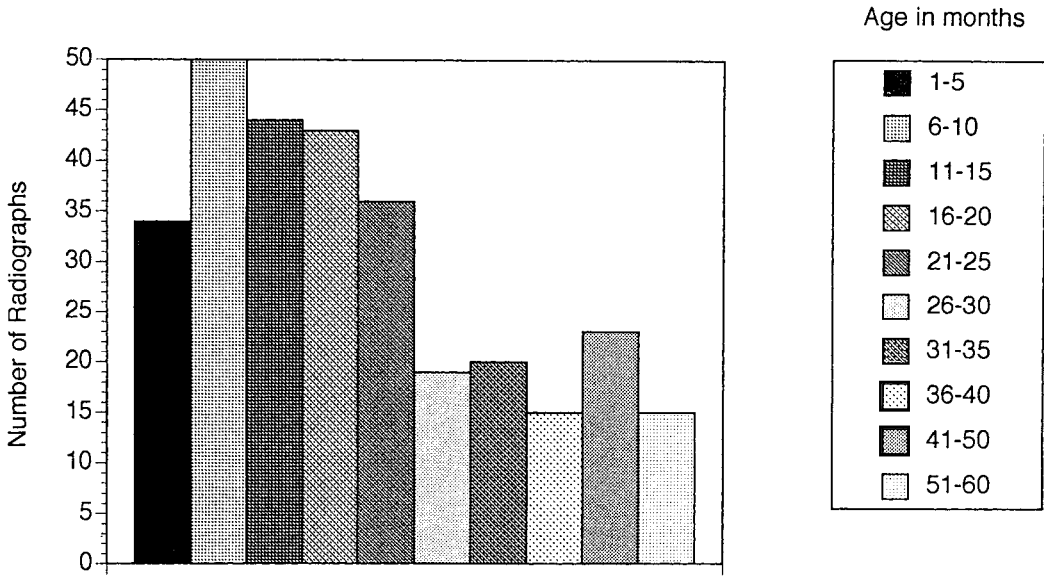


Fig. 2. Sample of chimpanzee radiographs utilized in this study. This mixed longitudinal sample comprises 299 lateral head radiographs from 33 lab-born and reared chimpanzees of known chronological age.

opment based on living apes and humans, such as those presented here.

MATERIALS AND METHODS

This study is based upon radiographs housed in the Department of Anthropology at the University of Pittsburgh and taken on 33 lab reared chimpanzees at the Southwest Foundation for Biomedical Research, San Antonio, Texas ($N = 16$), and the Laboratory for Experimental Medicine and Surgery in Primates of the New York University School of Medicine, New York ($N = 17$). The Pittsburgh chimpanzees are part of experimental studies of anterior maxillo-facial growth mechanisms (Siegel, 1978; Siegel and Sadler, 1979, 1981; Siegel et al., 1990, 1992; Mooney et al., 1991a,b). As part of these studies, the animals were periodically sedated and radiographed in a head holder at a constant distance from the film and X-ray source. The current sample includes 299 lateral head radiographs from 33 chimpanzees, taken at irregular intervals from 3 months of age to nearly 5 years of age (Fig. 2). The radiographs were scored by the first author using an 8 stage scale of molar development

TABLE 1. Description of developmental stages of molar teeth in Pan troglodytes

Stage	Description
A	Initial cusp calcification is visible as one or a series of small inverted cones in the upper part of the crypt; there is no fusion of these points
B	Initial points of calcification are fused, forming a regularly outlined occlusal surface
C	Enamel formation is completed at the occlusal surface with extension towards the cervical region; dentine deposition has begun below the enamel crown, and the pulp chamber has a smoothly curved superior border
D	Crown is completely calcified to the cementoenamel junction and the beginnings of root formation are present in the form of a spicule
E	Radicular bifurcation is visible while root length is always less than crown height
F	Radicular bifurcation is further developed, giving the roots a funnel shape; root length is equal to or greater than crown height
G	Root canals are parallel sided with open apices
H	Completion of root length marked by apical closure

(Fig. 3 and Table 1) modified from Demirjian's (1986) work on human dentition. The first four stages describe the development of the tooth crown from initial calcification (A) to completed crown formation (D). The next four stages reflect increasing growth in root length (E-G) and culminate in apical root

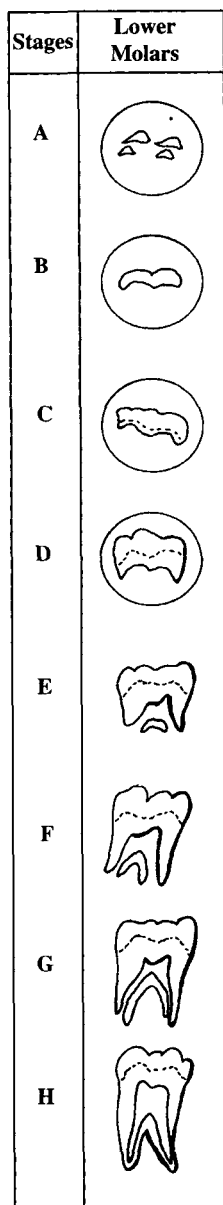


Fig. 3. Eight stages of molar development used in studies of chimpanzee dental development, modified from a similar set of stages developed by Demirjian (1986) for human dental development. Stages A–D track calcification of the tooth crown and Stages E–H track development of the root. See Table 1 for a complete definition of each of these stages.

closure (H). As is typical in longitudinal growth studies, the age at which a stage was attained was recorded as the average of the animal's age at the first radiographic appearance of each dental stage and its age in the previous radiograph. We also identified the onset and completion of crown and root development for the antemolar teeth. All radiographs with visible and scoreable teeth were included in the analysis, providing information on the variability inherent in chimpanzee dental development. Estimates of central tendency (mean) and of dispersion (standard deviation) were calculated for age at first appearance of each molar developmental stage and the results were compared with those from an earlier study, based on a different sample of chimpanzees (Anemone et al., 1991). Antemolar teeth were tracked as far as onset and completion of crown and root development. Currently, the molar data are complete for Stages A–H of the first molar, Stages A–E of the second molar, and Stages A,B of the third molar.

EXPERIMENTAL TREATMENT AND STATISTICAL ANALYSIS

Since these animals were subjects of certain experimental procedures, a brief discussion of these procedures and their potential effects (if any) on molar development is warranted. The experiments involved 4 different surgical procedures on the maxillo-facial region of some of the chimpanzees. Animals were assigned to 1 of 6 different experimental groups: a control group which experienced no surgical intervention (Group 6, $N = 7$), a sham surgery control group (Group 5, $N = 5$) whose members were anesthetized and had elevation but not resection of the septomaxillary ligament performed, and 4 surgical groups. The surgical procedures were premature fusion of the premaxillary-maxillary suture (Group 1, $N = 4$), resection of the septo-premaxillary ligament (Group 2, $N = 5$), removal of the middle three fourths of the cartilaginous nasal septum (Group 3, $N = 8$), and resection of the septo-premaxillary ligament and premature fusion of the premaxillary-maxillary suture (Group 4, $N = 4$).

A series of statistical tests were conducted

TABLE 2. Student's *t*-tests for age in months at first appearance of mandibular molar stages of surgical and non-surgical groups

Tooth stage	Surgical			Non-surgical			<i>P</i> value ¹
	mean	S.D.	N	mean	S.D.	N	
M1A	3.78	.87	19	4.29	1.38	9	.24
M1B	8.94	1.90	21	9.20	2.75	11	.75
M1C	14.39	2.15	19	15.01	1.89	9	.47
M1D	20.46	3.27	16	20.65	2.40	7	.89
M1E	28.45	4.33	15	28.05	1.38	5	.85
M1F	35.68	5.28	13	37.09	2.88	4	.62
M1G	44.42	5.88	10	43.03	2.94	4	.67
M1H	53.93	1.05	2	52.73	2.10	2	.54
M2A	15.71	3.60	20	15.58	2.61	8	.93
M2B	23.60	2.91	15	22.34	3.40	6	.40
M2C	32.90	4.68	14	30.37	3.19	5	.28
M2D	42.26	4.68	10	40.04	4.48	4	.43
M2E	53.93	1.05	2	53.69	2.23	3	.90
M3A	42.53	3.29	8	46.01	4.58	4	.16
M3B	55.18	3.51	3	51.24	NA	1	NA

¹ Results of 2-tailed student's *t*-test comparing surgical groups (Groups 1–4) and non-surgical groups (Groups 5, 6). No statistically significant differences ($P < .05$) were found. See text for discussion of the six experimental groups involved in this study. NA = not able to calculate.

TABLE 3. Analysis of variance for age in months at first appearance of mandibular molar stages

Tooth stage	Experimental group means						<i>P</i> value ¹
	1	2	3	4	5	6	
M1A	4.06	4.16	3.13	4.00	4.49	4.05	.43
M1B	9.44	9.06	7.98	10.18	9.75	8.74	.62
M1C	14.53	14.15	14.64	14.07	14.11	15.73	.85
M1D	22.37	18.73	20.43	20.23	19.90	21.66	.65
M1E	31.09	28.88	28.14	25.60	28.38	26.75	.53
M1F	36.87	36.79	31.18	34.50	37.09		.81
M1G	48.48	45.85		40.45	43.03		.21
M1H		53.19		54.67	52.73		.80
M2A	13.91	15.28	17.99	14.07	14.57	16.59	.28
M2B	23.93	23.16	23.60	23.73	21.77	23.46	.95
M2C	34.64	32.27	33.53	31.49	31.27	26.75	.72
M2D	43.13	43.85		40.40	40.40		.67
M2E		53.19		54.67	53.69		.90
M3A	41.72	43.85		41.74	46.01		.51
M3B	56.91	54.31			51.24		.37

¹ *P*-values are based on *F*-tests. Results indicate no statistically significant differences between experimental groups. Blanks are missing values. See text for discussion of the six experimental groups involved in this study.

on the age at first appearance of molar stage data in order to test the null hypothesis that these surgical interventions had no effect on the timing of molar development (Tables 2–4). The animals were first divided into two groups, the first including all 4 surgical groups and the second including the control groups (i.e., sham and control). Both parametric (Student's *t*, Table 2) and non-parametric (Mann-Whitney *U*) statistical tests indicated a lack of statistically significant differences in mean age at first appearance of molar stages between these two groups. Next, all 6 groups were compared by both parametric (ANOVA, Table 3) and

non-parametric (Kruskal-Wallis) methods. Again, no significant differences were found among the different groups. Finally, coefficients of variation (CV) for the original 6 groups and combinations thereof were calculated and compared (Table 4). If the “artificial” groups (e.g., surgical, non-surgical, and the entire sample) were drawn from statistically different populations with respect to mean age at attainment of molar stages, we would expect that the CVs for these groups would be much larger than for the original 6 groups. Examination of the data reveals that this is not so. The range of CV values for the surgical and non-surgical groups as

TABLE 4. Coefficient of variation of age in months at first appearance of mandibular molar stages for all groups¹

Tooth stage	Experimental groups								
	1	2	3	4	5	6	1-4	5, 6	1-6
M1A	30.3	23.4	13.8	11.7	16.8	50.5	23.0	32.2	26.9
M1B	33.7	9.5	17.9	18.0	18.2	39.7	21.3	29.9	24.2
M1C	15.2	15.9	14.7	20.4	16.0	8.7	15.0	12.6	14.1
M1D	18.3	14.1	12.2	21.5	12.7	10.3	16.0	11.6	14.5
M1E	8.3	22.7	13.6	10.7	4.8		15.2	4.9	13.3
M1F	6.3	24.0		11.6	7.8		14.8	7.8	13.3
M1G	4.5	18.1		10.1	6.8		13.2	6.8	11.7
M1H					4.0		1.9	4.0	2.9
M2A	5.4	23.2	23.7	20.4	24.3	4.9	22.9	16.8	21.1
M2B	12.6	17.3	5.1	18.2	18.7	8.6	12.3	15.2	13.0
M2C	9.9	12.5	10.0	23.7	9.1		14.2	10.5	13.7
M2D	10.2	11.1		13.4	11.2		11.1	11.2	11.0
M2E					4.2		1.9	4.2	3.1
M3A	6.7	11.1		5.0	10.0		7.7	10.0	9.0
M3B		2.9				3.4		4.6	

¹ Coefficient of variation (CV = [standard deviation/mean]*100) compared for individual groups (Groups 1-6), surgical (Groups 1-4) and non-surgical groups (Groups 5, 6), and the entire sample. See text for discussion of the six experimental groups involved in this study. Blanks could not be calculated.

well as for the entire lumped sample fall comfortably within the range of CV values for the 6 experimental groups.

Thus, each of these statistical approaches fails to disprove the null hypothesis, and thus supports the conclusion that the experimental procedures have had no significant effects on the timing of molar development in these animals. Consequently, we treat the entire sample of radiographs as a single population. These results are not surprising since all of the surgical procedures involve structures far removed from the developmental molar "field." While these procedures affected the growth and development of structures in the anterior cranio-facial region (Siegel, 1978, 1980; Siegel and Sadler, 1981; Siegel et al., 1990, 1992; Mooney et al., 1991a,b) and the growth of the posterior midface (Siegel et al., 1990, 1992), they have apparently had no discernible effects on the development of the molar dentition.

RESULTS

Means and standard deviations for age at first appearance of mandibular molar stages among the Pittsburgh chimpanzees are presented in Table 5 and illustrated in Figure 4. Several interesting aspects of pongid dental development are illuminated by these data. The duration of crown calcification for the first two molars, and of root calcification for the first molar, can be estimated. The first molar crown calcifies in slightly less than,

and the second molar crown in slightly more than, 2 years, while the first molar root develops in approximately $2\frac{1}{2}$ years. The first molar is radiographically present at birth in both humans (Moorrees et al., 1963) and chimpanzees (Anemone et al., 1991), and thus the age at Stage A for the first molar (3.95 months) is an overestimate due to the absence of calcification data on prenatal specimens in this study. For each of these parameters of dental development, the results of this study support the results of Anemone et al. (1991) based on the smaller Yerkes sample of chimpanzees. In that study, the first molar crowns were estimated as developing between birth and 2 years of age, with the M1 roots completing their development at around 5 years of age. The second molar crowns in the Yerkes chimpanzees developed between around 18 and 48 months, and the third molar crowns initiated calcification at around 48 months.

The data from the Pittsburgh chimpanzees also clearly indicate significant temporal overlap in the calcification of adjacent molar crowns in chimpanzees, and in this respect, present a very different picture of molar development than that presented by Dean and Wood (1981). The crown of the first molar reaches Stage D (i.e., crown completion) at an average age of 20.52 months (s.d. = 2.98 months), while the crown of the second molar begins calcification at an average age of 15.67 months (s.d. = 3.30

TABLE 5. Age at first appearance of mandibular molar stages in *Pan troglodytes*¹

Stage ²	M1			M2			M3		
	Mean	S.D.	N	Mean	S.D.	N	Mean	S.D.	N
A	3.95 ³	1.06	28	15.67	3.30	28	43.69	3.94	12
B	9.03	2.19	32	23.24	3.02	21	54.19	2.49	4
C	14.59	2.06	28	32.24	4.40	19	NA		
D	20.52	2.98	23	41.62	4.57	14	NA		
E	28.35	3.77	20	53.78	1.67	5	NA		
F	36.01	4.78	17	NA			NA		
G	44.02	5.13	14	NA			NA		
H	53.33	1.52	4	NA			NA		

¹Age at first appearance of dental stages is calculated as the mean of an individual's age in months when a dental stage first appears radiographically and the individual's age at the time of the previous radiograph.

²Dental stages are fully described in the text. Stage A represents initial calcification of crown, Stage D represents crown completion, and Stage H represents apical closure of root.

³This is a biased estimate of M1 first appearance owing to the lack of prenatal data. See text for discussion.

NA, Data not available.

Molar Crown Calcification *Pan troglodytes*

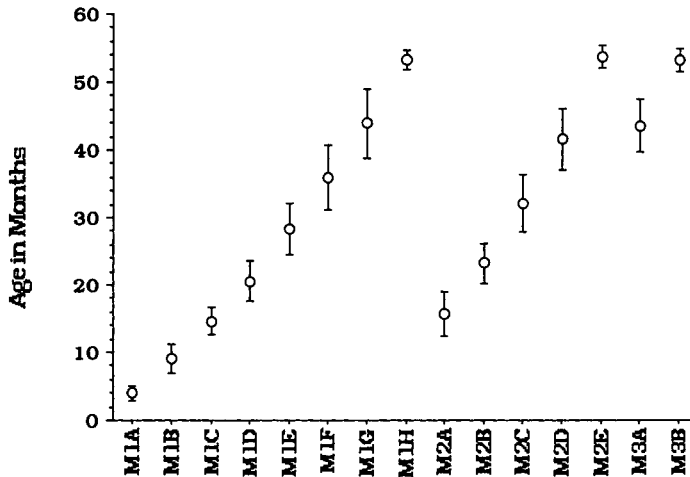


Fig. 4. Mean and one standard deviation range for age at first appearance of molar dental stages in the Pittsburgh sample of chimpanzees. Data are complete (i.e., including Stages A–H) only for the first molar. Comparison of Stages A and D for adjacent molars clearly

indicates the temporal overlap that characterizes calcification of these tooth crowns in chimpanzees. The data upon which this chart is based are presented in Table 5. For comparison with the pattern of molar crown calcification in modern humans, see Figure 5.

months). Similarly, the third molar crown first appears radiographically (i.e., Stage A) at an average age of 43.69 months (s.d. = 3.94 months), while the second molar completes its calcification at 41.62 months (s.d. = 4.57 months). Again, these results provide supporting evidence for the identification of temporal overlap in calcification of the crowns of adjacent molars in the Yerkes sample of chimpanzees (Anemone et al.,

1991). Unlike Dean and Wood's (1981) suggestion of equal and consecutive periods of molar crown development among apes (i.e., M1 between birth and 2.5 years, M2 between 2.5 and 5 years, M3 between 5 and 7.5 years), this overlapping pattern of adjacent molar crowns presented here allows easy discrimination between a typically pongid and a human pattern of molar development. Data from Moorrees et al. (1963) suggests that

TABLE 6. Age at radiographic initiation and completion of mandibular molar crowns in *Homo sapiens*

Stage ¹	M1		M2		M3	
	Mean	S.D.	Mean	S.D.	Mean	S.D.
Crown initiation	Birth ²	0.1	3.7	0.4	9.3	1.0
Crown completion	2.25	0.3	6.5	0.7	12.0	1.3

¹Crown initiation is equivalent to Stage A as defined in the present study; crown completion to Stage D.

²The first molar is radiographically present at birth; all other figures are postnatal ages in years. Data presented are approximate means and standard deviations drawn from published charts (Moorrees et al., 1963) based upon longitudinal analysis of lateral radiographs of 246 middle class, white children from Ohio (136 males and 110 females).

long temporal gaps between the onset of calcification of adjacent molar crowns are common for North American white children of middle socioeconomic status (Table 6 and Fig. 5). This conclusion is supported by examination of approximately 75 panoramic dental radiographs of mostly white children between the ages of 10 and 16 from western New York (Anemone, unpub.). In this data set, 14 radiographs document a temporal gap between crown completion of M2 and initiation of calcification of the M3 crown. In none of these radiographs is there any evidence of initiation of M3 crown calcification prior to crown completion and substantial root development on M2. While some human populations may differ from the pattern described here for Europeans, our knowledge of dental development in non-Caucasian populations is extremely limited. Fanning and Moorrees (1969) demonstrated that while M3 is greatly advanced in its development in Australian aborigines over Caucasians, the typical pattern among native Australians involves a brief temporal gap between the calcification of adjacent molar crowns (see Tables 1 and 2, Fanning and Moorrees, 1969). At crown completion of M1, 22 of 31 Australian aborigines (71%) have yet to begin calcification of the M2 crown. Similarly, at crown completion of M2, 49 of 57 individuals (86%) show no calcification for M3 (Fanning and Moorrees (1969). In spite of the current poor state of our knowledge of the range in dental development among different populations of *Homo sapiens*, it seems reasonable to conclude that the pattern of temporal overlap in calcification of adjacent molar crowns is one important

discriminator between human and pongid patterns of dental development.

Comparison of the stage of development of antemolar teeth, in particular the incisors and canines relative to that of the first molar illustrates another unique aspect of chimpanzee dental development. Although the lateral head radiographs available for these animals makes difficult any quantitative scoring of the development of the anterior teeth (and none was attempted in this study), crown and root initiation and completion for the incisors and canines can usually be noted. The typical pattern of antemolar tooth development seen in the Pittsburgh chimpanzees was extremely similar to that seen in the Yerkes chimpanzees (Anemone et al., 1991). That is, at emergence of the first molars (roughly Stage F–G for M1) at between 3 and 4 years of age, the incisor and canine crowns were still incompletely developed and no roots were visible (Fig. 6). Data on eruption of the permanent dentition in the Yerkes (Nissen and Riesen, 1964) and the LEMSIP chimpanzee samples (Conroy and Mahoney, 1991; Kuykendall et al., 1992) establishes that both incisors and second molars erupt close in time, between 6 and 7 years of age, while the first molar erupts at slightly more than 3 years of age. This pattern is clearly distinct from the human pattern, in which anterior teeth are crown complete with significant root development at M1 eruption (Conroy and Vannier, 1991a), and in which eruption of the incisors and the first molar occur relatively close in time (between 6 and 7 years of age) (Demirjian, 1986).

To summarize, these data indicate the presence of two important developmental patterns which we suggest serve to clearly distinguish chimpanzee dental development from that of modern humans. First, chimpanzees are characterized by marked temporal overlap in calcification of adjacent molar crowns. This is in direct contrast to the human pattern of moderate to long temporal gaps between the calcification of adjacent molar crowns (Demirjian, 1986; Fanning, 1961; Moorrees, 1959; Moorrees et al., 1963). The second major developmental difference concerns the stage of development of the anterior teeth relative to the molars. At M1

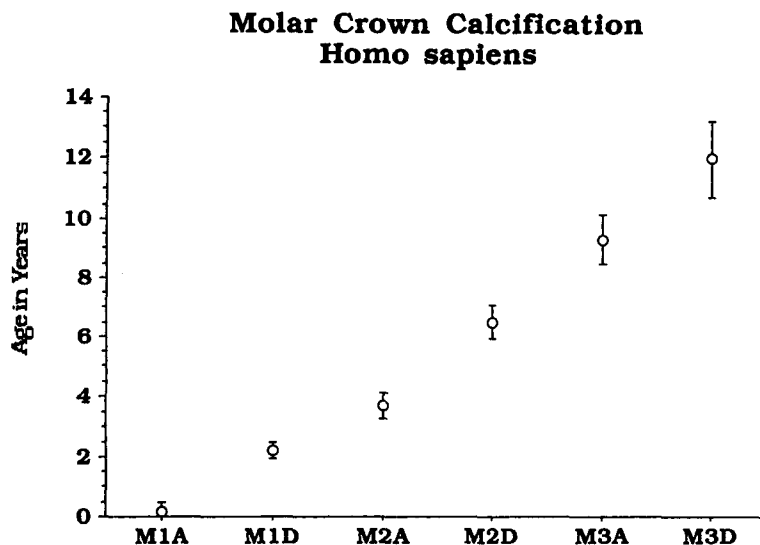


Fig. 5. Age at first appearance of molar developmental stages in modern humans based on a white, middle class population from Boston (Moorrees et al., 1963). Means and one standard deviation range are presented for crown initiation (Stage A) and crown completion (Stage D) to illustrate the temporal gap between calcification of adjacent molar crowns. The data upon which this chart is based are presented in Table 6.

emergence in *Homo sapiens*, all the anterior teeth have completed crowns and most have significant root development (Demirjian, 1986), while at the same point in relative posterior tooth development among chimpanzees (i.e., at M1 emergence), anterior teeth are much less advanced, most having incomplete crowns and none having any significant root development. Human dental development is characterized by the emergence of the central incisor and the first permanent molar at roughly the same time (between 5 and 7 years of age), while the central incisor emerges closer in time to that of the second molar among apes (between 6 and 7 years of age). Thus we can conclude that at emergence of the first molar, human anterior teeth are developmentally advanced compared to chimpanzees, or conversely, that human molar development is delayed compared to that of the chimpanzee. In fact, the relative amount of time allotted for incisor development is between 6 and 7 years in both chimpanzees and humans (Anemone et al., 1991; Demirjian, 1986). The differences arise mainly as a result of the enormously prolonged developmental period of the hu-

man first molar and especially its root, which develops in about 7 years versus approximately 3 years in chimpanzees. It is, therefore, more accurate to conclude that human molar development is delayed compared to that of apes.

EARLY HOMINID DENTAL DEVELOPMENT

The evolutionary significance of the differences between human and ape dental development lies in the application of these data to comparative studies of the developing dentitions of Plio-Pleistocene hominids. The recent application of high-resolution computed tomography (CAT) to image the developing dentitions of fossil hominids has done much to clarify our understanding of the characteristic patterns of dental development in human evolution (Conroy and Vannier, 1987, 1988, 1989, 1991a,b). A topic of long-standing controversy in the paleoanthropology literature (e.g., Broom and Robinson, 1951; Conroy, 1989; Dean, 1985a; Grine, 1987) is the timing of calcification and emergence of the first permanent molar and

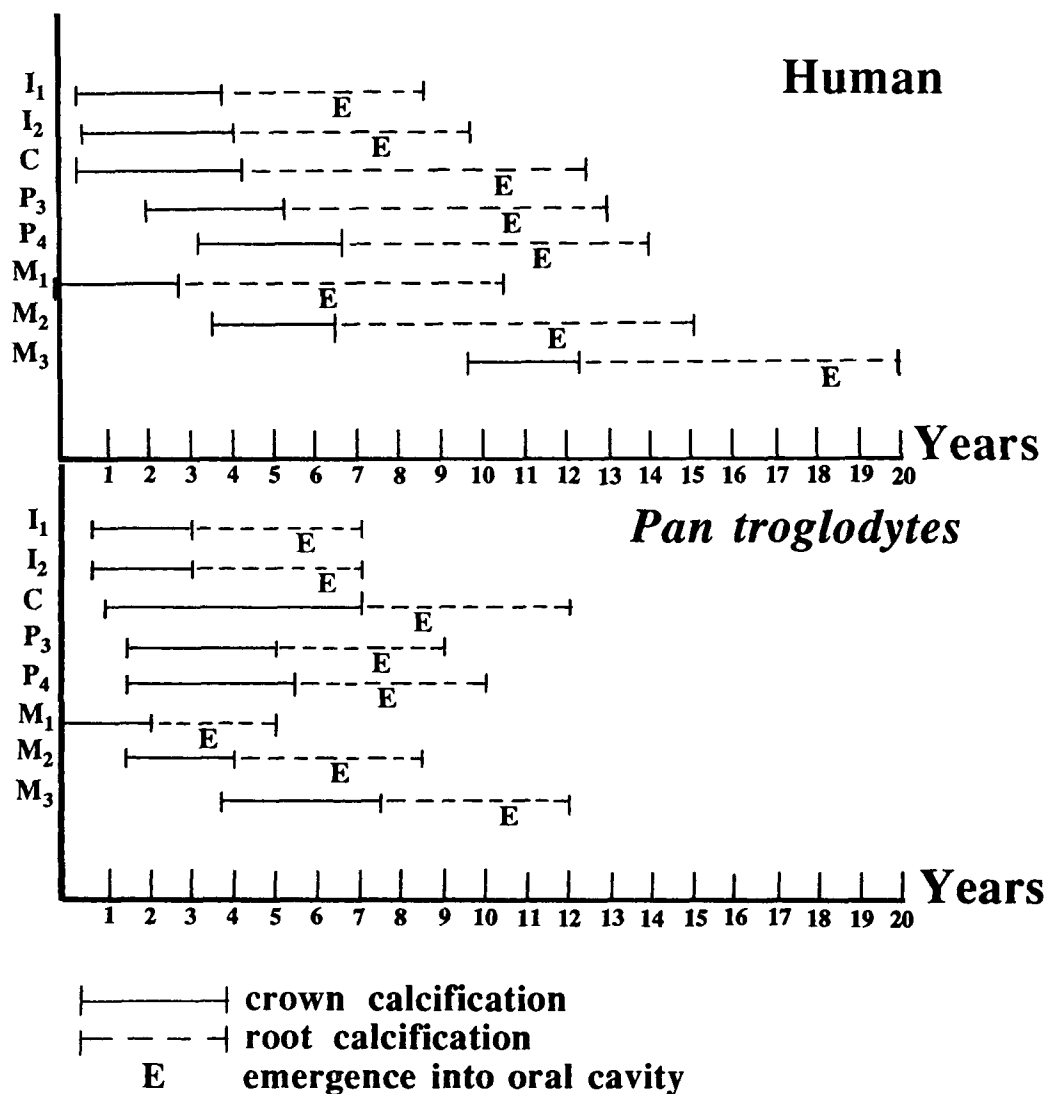


Fig. 6. Comparison of the developing dentition in humans and chimpanzees. The human chart is redrawn from Dean and Wood (1981); the chimpanzee chart is redrawn from Anemone et al. (1991), based upon an earlier study of a mixed longitudinal sample of 99 radiographs from 16 chimpanzees of known chronological age, born and reared at the Yerkes Primate Research Center.

the central incisor among the australopithecines. As mentioned above, delays in the development of the molar series among humans result in close synchrony in the emergence of these teeth into the oral cavity between 5 and 7 years of age. Among apes, the central incisor emerges closer in time to the emergence of the second molar, due to the relatively and absolutely advanced de-

velopment of the ape molar dentition. Conroy and Vannier (op. cit) have clearly demonstrated that robust australopithecines from Swartkrans resembled modern humans in central incisor-first molar emergence pattern, while gracile australopithecine remains from both Taung and Sterkfontein more closely resemble the ape pattern. This supports earlier suggestions of a similar di-

chotomy among australopithecines by Smith (1986) and Dean and coworkers (Beynon and Dean, 1988; Beynon and Wood, 1987; Bromage, 1987; Bromage and Dean, 1985; Dean, 1985b, 1987a,b). Some evidence also suggests the presence of different patterns of adjacent molar crown development among robust and gracile australopithecines. Conroy and Vannier (1991a) present CT scans for several gracile australopithecines (e.g., Taung, STS 24, STS 2) that demonstrate an overlapping pattern of adjacent molar crown calcification, while several robust australopithecines (e.g., SK 63, SK 64) would seem to have been characterized by temporal gaps between the calcification of adjacent molar crowns. Having established the pattern of australopithecine dental development, however, we are still no closer to understanding the timing of that development.

The best approach to the actual timing of ontogenetic development among australopithecines is to be gained by studies of enamel incremental markers including cross striations, which reflect daily increments of enamel formation, and striae of Retzius, reflecting a roughly weekly periodicity of unknown origin (see Dean, 1987b; and Mann et al., 1990, for recent reviews). A series of studies of enamel incremental markers suggest that australopithecine crown calcification times were more rapid and that ages at death were younger than previous estimates (Beynon and Dean, 1987, 1988; Beynon and Wood, 1987; Bromage, 1987; Bromage and Dean, 1985; Dean, 1987a,b). Early hominids were apparently erupting their first molars at between 3 and 4 years of age. However, the gracile australopithecines were following an apelike pattern of advanced molar development relative to anterior teeth with temporal overlap between adjacent molar crowns, while the robust australopithecines were following a delayed pattern of molar development similar to that seen in modern humans. Thus, regardless of an apparently apelike or human pattern of dental development, the absolute time frame of australopithecine dental development appears to have more closely resembled that of modern apes than humans, implying that extended periods of childhood dependency did not characterize australopithecine ontogeny. Clearly, pattern

and timing of dental development were decoupled among Plio-Pleistocene fossil hominids. These conclusions seriously question any reconstruction of the behavior and biology of australopithecines in a fully hominized fashion, and suggest that Plio-Pleistocene hominids were living prior to the shift to the extremely prolonged ontogeny that characterizes modern humans and that may be associated with language, tool manufacture and culture.

Finally, the functional and evolutionary significance of the presence of both apelike and human patterns of dental development in fossil hominids must be addressed. We know very little about the functional significance of the different dental developmental patterns seen in gracile and robust australopithecines. Simpson et al. (1990) have suggested that this dichotomy may be functionally correlated with the more orthognathic face of robust australopithecines and humans when compared to the more prognathic face of gracile australopithecines. This is an important question that warrants further consideration and that would probably be amenable to experimental analyses. Concerning the phylogenetic significance of molar developmental patterns, Conroy and Vannier (1991a) have suggested that the apelike pattern is primitive and the human pattern derived. Using the histological evidence that robust australopithecines had very rapid rates of enamel formation on the crowns of their anterior teeth (Dean, 1987a, 1989; Beynon and Dean, 1988), Conroy and Vannier (1991a:154) suggested that the shift from a primitive to a derived character state for I1-M1 pattern could have occurred in two different ways: "1) by accelerating the maturation of anterior teeth relative to molars or 2) by delaying maturation of molars relative to anterior teeth." They cogently suggest that the evidence supports the hypothesis that robust australopithecines achieved the "human" pattern by the first method (i.e., accelerating the development of anterior teeth), while humans used the second method (i.e., delaying the development of posterior teeth). Consequently, this similarity between robust australopithecines and humans is convergent and of no phylogenetic importance. Functional understanding of

these convergent similarities and of the meaning behind the pattern distinction in dental development between gracile and robust australopithecines remain fertile areas of study. The importance of a clear understanding of pattern and timing differences in dental development between apes and humans remains a critical foundation for explorations of the developmental history of our fossil ancestors.

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